Wilson Bull., 91(3), 1979, pp. 434–440

RESPONSE TO FOSTER NESTLINGS BY RED-WINGED BLACKBIRDS AT DIFFERENT REPRODUCTIVE STAGES

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Some investigators have performed experiments on acceptance of foster young in the nests of non-passerines. They report differences in acceptance in such stages as early egg-laying, incubation or prolonged incubation (Breitenbach et al. 1965, Beer 1966, Miller 1972). The only passerine data available were those collected by Emlen (1941) on the Tricolored Blackbird (*Agelaius tricolor*) and by Holcomb (1967) on the American Goldfinch (*Carduelis tristis*). The goldfinches, with a normal incubation of 11–12 days, accepted young after 5 and 19 days of incubation, respectively, and raised them to fledging.

Emlen (1941) reported that Tricolored Blackbirds fed young that hatched in the nest as early as the last day of egg-laying. Nestlings 2–3 days of age were placed in 10 nests where laying had just been completed. Two females abandoned their nests, but 8 females cared for the nestlings. Emlen also showed that females brought very little food to the nest until they finished laying. He concluded that development of breeding behavior in the tricolor is closely regulated by physiological factors from the start of nest-building through initiation of incubation, and largely by external situations associated with the nest during the rest of the cycle.

This paper describes experiments conducted to test the effects of foster nestlings of different ages on parental acceptance in periods of egg-laying, normal incubation, or prolonged incubation in the Red-winged Blackbird (*Agelaius phoeniceus*). This paper will deal with the observation of acceptance, non-acceptance or aggressive behavior toward nestlings followed by acceptance. It does not analyze the intricate behavior of development of brooding and feeding.

My hypotheses were (1) that acceptance of nestlings during the empty nest and egg-laying periods would be the same as during the normal incubation period and (2) that acceptance of nestlings during the prolonged incubation period would be the same as during the normal incubation.

METHODS

Red-wings were studied from 1966–1970 in small marshes and alfalfa fields at Fremont, Dodge Co., Nebraska in 1966; Wooster, Ohio in 1967 and near Waterloo, Douglas Co., Nebraska from 1968–70. Each year several hundred nests were observed. The large number of nests observed provided (1) documentation of normal abandonment rate and (2) nests from which nestlings could be transferred to other nests in different stages.

TABLE 1

DISTRIBUTION OF RED-WINGED BLACKBIRD NESTS IN WHICH EXPERIMENTS WERE PERFORMED WITH FOSTER NESTLINGS

Time in cycle	Day 0–1 nestlings	Day 2–5 nestlings	Day 6–9 nestlings
Nest complete	–	1	1
Egg-laying: day 1	1	7	4
2nd to last	3	5	3
next to last	4	6	4
last	3	1	2
Normal incubation: day 1–3	14	1	1
4–9	9	–	1
Prolonged incubation: day 13–15	1	1	1
16–18	3	–	2
19–22	7	3	5

Females were induced to incubate beyond the normal time by placing artificial eggs of the same size, shape and color as their own into the nests early in incubation.

Nestlings introduced to foster nests were separated into 3 age groups: (1) nestlings that hatched from eggs in the nest or were transferred at day 0 (day of hatching) or day 1, (2) days 2–5, and (3) days 6–9. Nests into which these nestlings were introduced were categorized as shown in Table 1. Transfers of nestlings consisted usually of the normal brood size of 3 to 4 nestlings but occasionally of only 1 or 2.

Altogether, 140 transfers of young were made but inconclusive results were obtained in 46 cases, primarily due to predation or severe climatic conditions. Nestlings remained in the foster nest until acceptance or non-acceptance was established in studies from 1966–1969. As there were 3 cases of severe aggressive behavior toward young in those 4 years, I adopted a different procedure in 1970 to protect nestlings from injury. I placed nestlings in a foster nest for a 3–5 h period and either watched the nest from a concealed point or returned to it and removed the young. There were no cases of aggressive behavior in 1970. In all 5 years of the study, nestlings in foster nests were examined carefully each day following their introduction to determine whether or not they had been injured, fed or brooded by foster parents. For statistical evaluation of these data I used a Chi-square test of independence.

RESULTS

There were only 5 nests of a total of 94, or 5.3% of the foster nests, where the nestlings were abandoned or were pecked severely by the adults (Table 2). I do not know whether the nestlings were attacked by the male or female. The female is more suspect as males seldom visited the nests.

Table 2 shows that 4 of the 5 cases of abandonment or severe aggression came just previous to or during the egg-laying period. Table 2 shows the

TABLE 2

RELATIONSHIP BETWEEN REPRODUCTIVE STAGE AND FREQUENCY OF AGGRESSION TOWARD, OR ABANDONMENT OF FOSTER NESTLINGS BY RED-WINGED BLACKBIRD FEMALES

Stage	No. of nests	Severe aggression (%)[a]	Abandonment (%)
Egg-laying (immediately before or during)	45	6.5	2
Normal incubation	26	0	0
Prolonged incubation	23	0	4

[a] These nestlings were gradually accepted even though attacked when first placed in the nest.

1 other abandonment, which occurred on day 18 in prolonged incubation. Three of the 4 cases that occurred previous to normal incubation involved an aggressive pecking of the nestlings by a parent previous to the time when egg-laying ceased and the incubation phase of the cycle began. The nestlings were later accepted and raised to fledging. The other case involved abandonment.

There was 100% acceptance of nestlings transferred to nests during the normal incubation period. We failed to reject the hypothesis that acceptance of nestlings previous to normal incubation was the same as during normal incubation ($P > 0.05$). We failed to reject the hypothesis that acceptance of nestlings during the prolonged period of incubation was the same as during the normal incubation ($P > 0.05$).

From a total of 94 nests, there were only 2 females that abandoned nests with foster young. There was no observed aggressive behavior in either case. From records of several years of field research on Red-winged Blackbirds I have no evidence of females abandoning nests because of my visits. The only nests that were abandoned were those where eggs were removed by a predator, eggs were broken by a predator or the female was captured by a predator. It is not unreasonable to suspect that 1 or 2 females from a total of 94 could have been killed by predators. It would be less reasonable to believe that both females were killed on the day when foster young were placed in the nest.

There was no trend established in acceptance of nestlings on the basis of age differences. However, some brief observations suggested that brooding and feeding of older nestlings were interfered with because of size. The females appeared frightened by the larger nestlings and initial feeding began after a longer elapsed time than with smaller nestlings. Although in most cases older nestlings were accepted (not injured and some feeding and

brooding done), often they lost weight because feeding rate was not sufficient. In some cases 1 or 2 of a group of 3 or 4 perished from starvation. When nestlings 5 days or less of age were introduced into 70 different nests, they appeared to receive sufficient food to maintain growth except in the 1 case of abandonment and in 1 case where day 5 nestlings were introduced on the first day of egg-laying.

In all 43 cases where nestlings were transferred to foster nests during egg-laying, even though the nestlings were brooded or fed, the female continued to lay until her full clutch was completed.

DISCUSSION

Holcomb (1968, 1970) reported that Red-winged Blackbird females incubate a mean of about 19 days on artificial eggs of normal or 1½× normal size, even though the normal incubation period is only 11 days. However, they incubate eggs ½× normal size an average of about 15 days, suggesting that red-wings do react to either a visual stimulus, a tactile stimulus or a combination of stimuli from the eggs.

The greater amount of data on abandonment collected for the red-wing during egg-laying and normal incubation appears similar to the limited data provided for Tricolored Blackbirds by Emlen (1941). There is no evidence of a difference in abandonment when comparing (1) egg-laying and normal incubation or (2) normal incubation with prolonged incubation.

When younger nestlings were introduced to foster nests they appeared to receive sufficient food. Older nestlings sometimes were accepted and fed but grew more slowly than they would have in their original nests. Some perished, indicating inability of the female to adjust quickly to the demands of large nestlings. My data suggest that feeding behavior must develop quantitatively with the development of nestlings, beginning slowly and increasing as nestlings grow older and demand more food.

In more than 1 case, when I placed older nestlings in nests, they were accepted and fed for 1–2 days before fledging, whereupon the female spent at least part of her time incubating the eggs again. I do not know whether these females fed the fledglings enough to maintain them, whether the male fed them, or if they perished.

There are some differences between passerines and some non-passerines in acceptance of foster young early in the incubation period. Evidence presented herein for all passerines tested to date shows acceptance of foster young early in the incubation period in the Tricolored Blaekbird, American Goldfinch and Red-winged Blackbird. This is in contrast to a report by Breitenbach et al. (1965) on the response of hen Ring-neeked Pheasants (*Phasianus colchicus*) to chicks introduced during normal or prolonged in-

cubation. None of 3 hens accepted chicks 12 days early, 3 of 8 accepted them 8 days early and 7 of 7 accepted them 4 days early. Four of 4, 6 of 6 and 2 of 2 accepted chicks 4, 8 and 12 days late, respectively. Miller (1972) reported that in Ring-billed Gulls (*Larus delawarensis*) when chicks were introduced in the first week of incubation, acceptance was irregular and temporary but that parents accepted chicks introduced after 8 days. When Emlen and Miller (1969) delayed hatching of Ring-billed Gulls only 3 to 8 days, 3 of 12 sets of parents abandoned the nests or tossed the chicks out of the nest. Of 14 cases of acceptance reported by Miller (1972) from a total of 24 experiments, 16 chicks were initially pecked by adults.

I do not intend this paper to be a complete review of endocrinological factors controlling the onset of parental behavior. However, since there was some aggression toward foster nestlings in the egg-laying period, some comment on endocrinological factors is appropriate.

Brant and Nalbandov (1956) documented the effect of estrogen and progesterone on oviduct growth in chickens. Lott and Comerford (1968) demonstrated in Ringed Turtle Doves (*Streptopelia risoria*) that initiation of parental behavior may be due to a combined effect of progesterone and prolactin; progesterone alone established brooding, while progesterone plus prolactin caused both brooding and feeding. Hansen (1966) reported the effect an external stimulus (the squab) has on prolactin production and/or release in Ringed Turtle Doves. In pigeons (*Columba* spp.) (Schooley 1937), hens (*Gallus* spp.) (Collias 1950), House Sparrows (*Passer domesticus*) (Vaugien 1955), Bank Swallows (*Riparia riparia*) (Petersen 1955), Tricolored Blackbirds (Payne 1969) and White-crowned Sparrows (*Zonotrichia leucophrys*) (Lewis 1975), the ovary has been reported to be regressed during the incubation period. Meier (1969) has shown the antigonadal effects of prolactin in White-throated Sparrows (*Zonotrichia albicollis*).

I found (Holcomb 1975) that red-wing females exhibit great changes in incubation patch tissues as nest building, egg-laying, normal incubation and prolonged incubation proceed. I showed (Holcomb 1968) that in the egg-laying period of red-wings, estrogen and perhaps progesterone are abundant as evidenced by large ovary size and large size of the oviduct. As soon as laying ceases, ovary and oviduct regress rapidly and remain small until 2–4 days past the length of the normal incubation period. Small increases in ovarian weight begin, and there is a significant increase in size of the oviduct and of ovarian follicles, previous to abandonment of the eggs in the prolonged incubation period.

I believe that prolactin suppresses ovarian size in and maintains incubation in red-wings following ovulation. I believe that the large size of the ovary when a nest has been constructed or when eggs are being laid indicates that

prolactin is not present in quantities sufficient to have an antigonadal effect on the ovary. I have shown (Holcomb 1974) that incubation develops gradually in the red-wing female throughout the egg-laying period. This may indicate initially small amounts of prolactin that gradually increase, finally causing rapid antigonadal effects after all large ovarian follicles have ovulated. During this dramatic change in internal stimuli and in environmental stimuli such as new nest and new eggs, there is a transition period when the female may be aggressive toward nestlings, abandon them or fail to feed them sufficiently to maintain growth.

Throughout the normal incubation period the antigonadal effect of prolactin continues, and incubation constancy is highest. As the female progresses into a prolonged incubation, prolactin remains an antigonadal agent; but as it slowly diminishes, the ovary begins growing again and is active in releasing a hormone or hormones as evidenced by the increase in size of the oviduct. At this time females are still capable of accepting nestlings, as prolactin still has some influence. Furthermore, a transition from the now-familiar nest and eggs to new stimuli (the nestlings) may be an easier behavioral adjustment than during the early portion of the nesting cycle.

Evidently, as long as incubation continues, prolactin is sufficient for the acceptance of red-wing nestlings, even though their initial food demands cannot always be met. Emlen and Miller (1969) suggest that once normal incubation has been established, internal stimuli may play a role but may not be as important as external stimuli. These hypotheses await testing through continued studies.

SUMMARY

Experiments were performed with Red-winged Blackbirds (*Agelaius phoeniceus*) at different reproductive stages to determine the frequency of parental acceptance of nestlings. Nestlings aged 0–1, 2–5, and 6–9 days were placed in nests where the nest was complete without eggs and when the last, next to last, and second to last eggs had been laid. Nestlings of these different groups were also placed in nests during normal and prolonged incubation.

There appeared to be no great differences in ability of females to accept any age group of nestlings. However, during the egg-laying period most females fed nestlings sparingly and sometimes were aggressive toward nestlings. The frequency of acceptance of nestlings did not differ significantly between (1) normal incubation and egg-laying periods and (2) normal incubation and prolonged incubation periods ($P > 0.05$). The internal physiological mechanisms and the external stimuli that may account for the observed differences in behavior are discussed.

ACKNOWLEDGMENTS

I wish to express gratitude for support of this research by the Chapman Fund of the American Museum of Natural History, New York.

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